

THE GENITALIA OF *ACANTHINULA ACULEATA*.

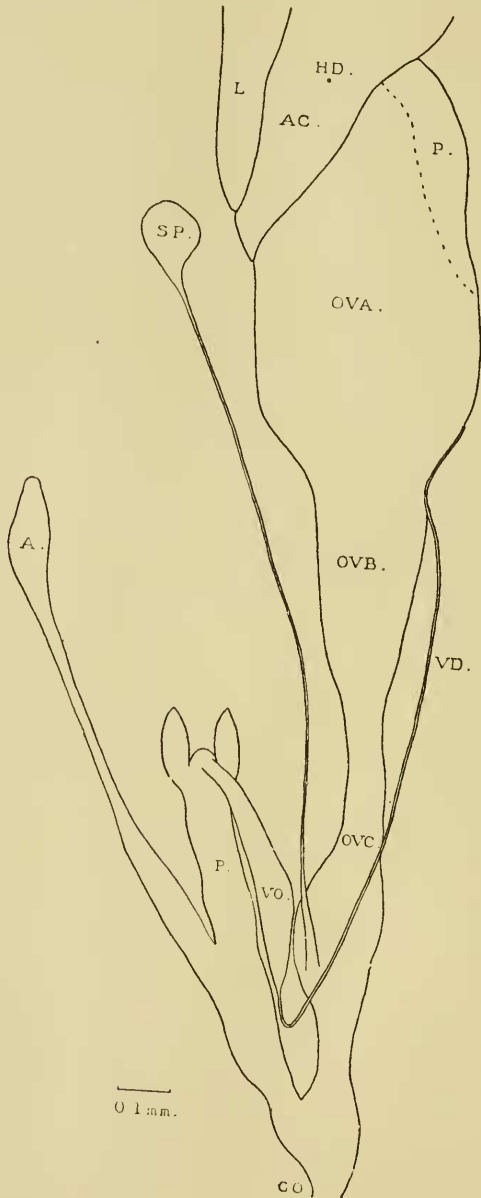
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THE following account of the genital apparatus of *A. aculeata* is based on the examination of twenty adult specimens from six localities, displayed by complete series of microscopical sections. The figure has been reconstructed from one such specimen, the parts being separated in the drawing so that they may be shown on conventional lines for easy comparison with other species. The male and female ducts diverge not far from the *genital orifice* (*GO*), and through the interval between them passes the right ocular retractor. The *penis* (*P*) in its lower part is generally similar in structure to the lower part of the oviduct without any particular abundance of muscular tissue; for a distance of about 0.1 mm. or rather less above the origin of the appendix (*A*) there is, however, a well-developed muscular sheath loosely embracing the organ. At its upper end the penis divides into three; on either side is a curious horn, the minute structure of which does not appear to differ materially from that of the upper part of the body of the penis and suggests no special function; the main channel of the penis continues upwards a little way beyond the origin of the horns and then curves over to join the vas deferens, which is embedded in the wall of the penis for some little distance below the actual junction. The *vas deferens* (*VO* and *VD*) loops round below in the customary fashion and is divided into two distinct parts, an ascending limb not much less bulky than the penis itself and a long (about 1.2 mm.), thin, descending limb lying in close relation with the oviduct into which it eventually opens above. The *appendix* to the penis (*A*) has a duct wide below and narrow above, and finally ends in a bulbous swelling, the terminal expansion being due as much to an increase in the substance of the wall as to a larger lumen. This appendix naturally lies folded up in a more or less complicated way, most commonly in a double M loop with the terminal bulb close to the upper end of the penis. Its minute structure is not suggestive of its function; I found no definite contents in the bulb. The *oviduct* (*OV*) may as usual be divided into three parts. Below is a simple conducting tube constituting the *free oviduct* (*OVC*). This expands above into the *glandular oviduct* (*OVB*), a wider tube with voluminous walls of mucinous cells, the lumen still remaining relatively simple: one small section of the wall forms a little recess lined with cubical, ciliated epithelium and lies in close relation to the upper end of the descending limb of the vas deferens, which eventually opens into it. Above the origin<sup>1</sup> of the vas deferens the oviduct expands still further and forms the complex folded *spermooviduct* (*OVA*) with massive mucinous walls. In the upper part there is

<sup>1</sup> The figure indicates the actual, not the superficial, origin of the vas.

the special mass of glandular tissue (*P*) with granular cells generally known as the *prostate*, the lumen opening into that of the spermoviduct.



The *hermaphrodite duct* passes into the substance of the albumen gland at the point shown in *HD*; it is sharply flexed on itself at the point of entry, though whether there is a definite vesicula seminalis is perhaps a question of terminology. The duct of the *spermatheca* (*SP*) arises rather low down on the free oviduct; it is long (about 1.4 mm.) and for the most part narrow, in its upper part not more than some 0.007 mm. wide over all. The globular spermatheca lies exceptionally high up, being overlapped by the lower ends of the *albumen gland* (*AG*) and *liver* (*L*). There are no traces of anything like a *dart-sac* or *mucous gland*, or other accessory organs on the female side.

My findings therefore correspond with those of Wiegmann, whose drawing was published posthumously by P. Hesse.<sup>1</sup> Wiegmann adds the statement, of which I have not been able to assure myself, that the retractor muscle is bifid, making attachment to the appendix as well as to one of the horns of the penis. The only detail in which my results differ is the relative length of the duct of the spermatheca, which I should be inclined to make longer than he does, but this is a difference which might be due to dissimilar methods if I am right in assuming that he was ingenious enough to arrive at his result by gross dissection.

How far these data serve to place *aculeata* in its correct taxonomic position I would not presume to say. The genitalia are certainly curious for one of the helicoids, in the absence of mucous glands and the presence of a penile appendix; among our native snails an appendix to the penis is most easily seen in *Ena*,<sup>2</sup> and similar appendices appear to occur in *Pupilla muscorum*, *Lauria umbilicata*, and *Vertigo minutissima*.<sup>3</sup> L. Germain<sup>4</sup> includes it in the "Pupidae" on the ground of its anatomical characters, which he does not detail. The radula is figured by E. W. Bowell,<sup>5</sup> who suggests a relationship to *Vertigo* for both *aculeata* and *lamellata*. How far *aculeata* is really close to *lamellata* is another question. The radulae (Bowell, loc. cit.) are in general similar but with well-marked differences, the shell of *lamellata* is rather peculiar in having no finished peristome, the genitalia are incomparable since I could find no male organs in *lamellata*,<sup>6</sup> the duct of the spermatheca is relatively much longer in *aculeata*, the "prostate" differs in its relation to the oviduct in the two species. Steenberg (loc. cit., p. 84) says, but without details, that the anatomy of the two species is different.

A hermaphrodite genital apparatus of this kind was found in nine out of the twenty specimens examined, but the male parts were absent from the other eleven. All the specimens were adult in the sense that the shells had a well-finished reflected peristome and rib, and were of adult dimensions (about 2½ mm. wide and high). Their

<sup>1</sup> Nachrichtsbl. Deutsch. Malak. Gesell., 1915, p. 56.

<sup>2</sup> See e.g. J. W. Taylor's figure in Monograph, vol. i, p. 361.

<sup>3</sup> C. M. Steenberg, *Danmarks Fauna: Landsnegle*, 1911, pp. 168, 170, 172; A. Moquin-Tandon, *Hist. Nat.*, vol. ii, 1855, p. 392, and pl. xxviii, fig. 1.

<sup>4</sup> *Mollusques de la France*, vol. ii, 1913, p. 190.

<sup>5</sup> Proc. Malac. Soc. Lond., vol. xi, 1914, p. 159; vol. viii, 1908, p. 127.

<sup>6</sup> *Journ. Conch.*, vol. xv, 1917, p. 175.

origins do not suggest any seasonal or local influence; eight of fourteen spring specimens and three of six collected towards autumn had no male organs. It is not that the male organs were rudimentary or ill-developed, they were not there at all, and the lower genitals were reduced to an oviduct and spermatheca, not different in any obvious way from those present in specimens with the full complement of male organs.<sup>1</sup> On the other hand, these individuals were not females, since in each one of the twenty specimens, whether the penis was present or not, plenty of eggs and spermatozoa were found in the hermaphrodite gland and duct.<sup>2</sup> Such an arrangement is remarkable and is, I think, unknown among the larger snails whose viscera are familiar.

LOCALITY.	DATE.	NUMBER OF SPECIMENS.	NUMBER WITH MALE ORGANS.
Rotherwas, Hereford.	April, 1915.	4	2
Aldenham, Herts.	Sept., 1915.	2	0
Radlett, Herts.	April, 1916.	1	0
Monks Risborough, Bucks.	April, 1916.	1	0
Rotherwas, Hereford.	April, 1916.	8	4
Great Hampden, Bucks.	Sept., 1916.	1	1
Scarborough, Yorks. <sup>3</sup>	Sept., 1916.	3	2
		20	9

The condition in these eleven specimens was in short similar to that found uniformly in twenty *lamellata*,<sup>4</sup> and its interpretation is equally difficult. They might be functionally only females; the presence of abundant spermatozoa is against this, though it is well known that in comparatively highly developed animals (*e.g.* frogs) the sexual glands may produce a certain number of gonads inappropriate to the sex of the individual. They might be self-fertilizing hermaphrodites; such is unusual, but is known to occur under stress of circumstances in a certain number of pulmonates,<sup>5</sup> and is a general possibility. They might be functionally both male and female, it being pretty clear that the vagina could function as an intromittent organ. They might be cyclically unisexual, though I think that any question of proterandry or proterogyny is excluded by the absence, rather than the presence in an atrophied condition, of the male organs, and by the abundance of spermatozoa. They might be abnormal abortive individuals, sexually impotent, a sort of

<sup>1</sup> The specialized segment of the wall of the glandular oviduct which is associated with the origin of the vas deferens was present, though not perhaps so fully developed as in those individuals in which that duct was found, and in some cases a short tag of vas deferens arising from it and soon ending blindly below.

<sup>2</sup> The spermatozoa were mostly in the duct. In one aphyllid specimen, a mass of spermatozoa extended from the upper part of the spermoviduct to near the genital orifice, and there were a few in the spermatheca, but it cannot of course be known where they came from.

<sup>3</sup> I am much indebted to Mr. J. A. Hargreaves for these specimens.

<sup>4</sup> *Journ. of Conch.*, vol. xv, 1917, p. 175.

<sup>5</sup> *Arion ater*, *Limnæa auricularia*, *L. pereger*, *Planorbis vortex*.

molluscan free-martin; it is difficult on this hypothesis to explain the normal structure of such organs as are present or the frequency of the condition.

The only anatomical point which I have observed which might help to a decision between these various possibilities is that the glandular organ with granular cells in connection with the spermoviduct, which is known as the prostate, was not found where the penis was absent. This suggests, though quite indefinitely, that these individuals were not functional males.<sup>1</sup>

Hermaphroditism is often associated with an indifferent capacity for locomotion, and it is a clear advantage to snails that, when two do happen to meet, both should be able to produce spermatozoa as well as eggs. Hence arises another consideration which may have to do with the absence of male organs. Large snails walk faster than small snails, and with very small species the rate of progression may become so slow that the chance of two individuals meeting becomes so trivial that it is not worth while to maintain an effective male copulatory apparatus. Locomotion becomes so slow that the habit of self-fertilization is added to the hermaphrodite structure. That dispersion of the members of a family from their birthplace is limited in the same way is no substantial objection to this view when we consider that the time devoted to sexual confluence is very small compared to that spent in wandering in search of food. It is perhaps also noteworthy that *aculeata* is not a gregarious species; the area in which it occurs may be circumscribed rather closely by environmental conditions, but the individuals generally occur in groups of one each, and the density of the population is low; it is not an "abundant" species as is often, e.g. *Carychium minimum*, in the same habitats.<sup>2</sup> As far as I know, *lamellata* has much the same habits, though it is perhaps more abundant where it occurs. In some other small snails gregarious habits render congress more likely, e.g. *Pyramidula rupestris*, *Pupa umbilicata*, *Vertigo* spp., and in these a penis is found, though whether in all specimens I do not know; male organs are also described in *Carychium*.

On the whole I incline to the speculative explanation that the aphyllic state is due to the simplification of structure which is necessarily associated with diminution in absolute size, that an animal cares more for what it does than for the apparatus by which it does it, and that both phallic and aphyllic forms are alike hermaphrodite and reproductive. The view that the possibilities of organic action are limited by narrow morphological boundaries has been productive enough along the line of phyletic speculation, but

<sup>1</sup> An organ of similar histological constitution is present in *lamellata*, but in connection with the lower part of the glandular oviduct, and hence possibly different in character; *aculeata* has nothing like it in the *lamellata* position.

<sup>2</sup> I am referring especially to dead leaves, particularly beech leaves, in woods. In the few specimens of *Punctum pygmaeum* from the same habitat which have been examined, no penis has been found.

it is essentially mechanistic in character, and fails to take into account the demonstrated capacity of living organisms to achieve their ends by self-regulated means. We should not, in other words, be too quick to assume that an *aculeata* is at any very grave disadvantage in maintaining its individuality and reproducing its kind because it has no penis; the majority, at any rate, of *lamellata* have abandoned that organ in favour of the roominess afforded by its absence, and reduced their genitalia to the simplest essentials.

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